Global leaf nitrogen and phosphorus stoichiometry and their scaling exponent

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Abstract: Leaf nitrogen (N) and phosphorus (P) concentrations constrain photosynthetic and metabolic processes, growth and the productivity of plants. Their stoichiometry and scaling relationships regulate the allocation of N and P from subcellular to organism, and even ecosystem levels, and are crucial to the modelling of plant growth and nutrient cycles in terrestrial ecosystems. Prior work has revealed a general biogeographic pattern of leaf N and P stoichiometric relationships and shown that leaf N scales roughly as two-thirds the power of P. However, determining whether and how leaf N and P stoichiometries, especially their scaling exponents, change with functional groups and environmental conditions requires further verification. In this study, we compiled a global data set and documented the global leaf N and P concentrations and the N:P ratios by functional group, climate zone and continent. The global overall mean leaf N and P concentrations were 18.9 mg g−1 and 1.2 mg g−1, respectively, with significantly higher concentrations in herbaceous than woody plants (21.72 mg g−1 vs. 18.22 mg g−1 for N; and 1.64 mg g−1 vs. 1.10 mg g−1 for P). Both leaf N and P showed higher concentrations at high latitudes than low latitudes. Among six continents, Europe had the highest N and P concentrations (20.79 and 1.54 mg g−1) and Oceania had the smallest values (10.01 and 0.46 mg g−1). These numerical values may be used as a basis for the comparison of other individual studies. Further, we found that the scaling exponent varied significantly across different functional groups, latitudinal zones, ecoregions and sites. The exponents of herbaceous and woody plants were 0.659 and 0.705, respectively, with significant latitudinal patterns decreasing from tropical to temperate to boreal zones. At sites with a sample size 10, the values fluctuated from 0.366 to 1.928, with an average of 0.841. Several factors including the intrinsic attributes of different life forms, P-related growth rates and relative nutrient availability of soils likely account for the inconstant exponents of leaf N vs. P scaling relationships.

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ABSTRACT

Leaf nitrogen (N) and phosphorus (P) concentration constrain photosynthetic and metabolic processes, growth, and productivity of plants. Their stoichiometry and scaling relationship regulate allocation of N and P from subcellular to organism even ecosystem levels, and are crucial to modelling plant growth and nutrient cycles in terrestrial ecosystems. Prior work has revealed a general biogeographic pattern of leaf N and P stoichiometric relationships and shown that leaf N scales roughly as 2/3 power of P. However, determining whether and how leaf N and P stoichiometry, especially their scaling exponent, change with functional groups and environmental conditions requires further verification. In this study we compiled a global data set and documented the global leaf N and P concentrations and the N:P ratios by functional type, climate zone, and continent. The global overall mean leaf N and P concentrations were 18.9 mg g^{-1} and 1.2 mg g^{-1}, respectively, with significantly higher concentrations in herbaceous than woody plants (21.72 mg g^{-1} vs. 18.22 mg g^{-1} for N; and 1.64 mg g^{-1} vs. 1.10 mg g^{-1} for P). Both leaf N and P showed higher concentrations at high than low latitudes. Among six continents, Europe had the highest N and P concentrations (20.79 and 1.54 mg g^{-1}) and Oceania had the smallest values (10.01 and 0.46 mg g^{-1}). These numerical values may be used as a base for the comparison of other individual studies. Further, we found that the scaling exponent varied significantly across different functional groups, latitudinal zones, ecoregions, and sites. The exponents of herbaceous and woody plants were 0.659 and 0.705, respectively, with significant latitudinal patterns decreasing from tropical to temperate to boreal zones. At sites with a sample size ≥ 10, the values fluctuated from 0.366 to 1.928, with an average of 0.841. Several factors including the intrinsic attributes of different life-forms, P-related growth rates and relative nutrient availability of soils likely account for the inconstant exponents of leaf N vs. P scaling relationships.

Keywords: Leaf, nitrogen, phosphorus, stoichiometry, scaling exponent, functional group

INTRODUCTION

Plant growth and metabolism depend on ribosome number and protein concentrations in living cells (Sterner & Elser 2002; Lambers *et al.* 2008). Nitrogen (N) and phosphorus (P), especially the N in Rubisco that drives photosynthesis and the P in rRNA that drives the generation and maintenance of proteins, are essential nutrients (Elser *et al.* 1996; Xie *et al.* 2003; Güsewell, 2004; Veneklaas *et al.* 2012; Ghimire *et al*. 2017) that are consequently tightly linked and important parameters in stoichiometric growth models (Ågren, 2004; Niklas *et al.* 2005; Elser *et al.* 2010). Therefore, the leaf N and P stoichiometric patterns including N and P concentrations and N:P ratios are largely explored both at regional and global levels (Reich & Oleksyn, 2004; Han *et al.* 2005; Sardans *et al.* 2015; Tang *et al*. 2017), which are important bridges linking elemental compositions or allocations with organismal metabolic processes and even energy flow in the whole ecosystem (Elser *et al*. 2010). In particular, the strong correlation between leaf N and P concentrations can be quantified via a stoichiometric

scaling relationship described by a power function as $N = \beta P^{\alpha}$, where α and β indicate the slope (i.e. the scaling exponent) and the "elevation" or *Y*-intercept (i.e. normalization constant), respectively, of the log-log linear leaf N concentration vs. P concentration regression line (Wright *et al.* 2004; Reich *et al.* 2010). As is the case for other allometric "rules" in ecology, leaf N vs. P scaling provides a simple but useful empirical model (Niklas *et al.* 2005; Reich *et al.* 2010; Elser *et al.* 2010) in which the exponent is considerably critical for predictions of plant and ecosystem functioning (Díaz *et al.* 2004). For example, a previous stoichiometric growth model (the growth rate hypothesis) posited that organisms with higher growth rates required disproportionately higher P than N concentrations resulting in a scaling exponent of N to P concentrations below unity (i.e. $\alpha < 1.0$) (Sterner & Elser 2002).

The large-scale patterns of the leaf N and P stoichiometry in relation to environmental conditions (especially temperature), biogeochemical gradients, intrinsic genetic factors and species composition have been generalized in previous studies (Reich & Oleksyn, 2004; Wright *et al.* 2005; Han *et al.* 2005; Han *et al.* 2011; Ågren & Weih, 2012; Sardans *et al.* 2015). Moreover, a constant exponent of leaf N vs. P scaling is appealing to and chased by ecologists for its simplicity in model operations. For example, empirical studies have reported that N concentrations scale, on average, across species as a 3/4-power function of the P concentrations (e.g. Niklas & Cobb 2005). If the invariant exponent is true, the plant growth rate could be predicted by leaf N and P stoichiometry (Niklas *et al*. 2005; Niklas, 2006). Nevertheless, a core issue remains — whether the N vs. P scaling exponent is invariably "constant", or whether its numerical value depends on species functional groupings or other ecosystem properties. Numerous studies have also reported N vs. P scaling relations with statistically significant variation in the scaling exponent (e.g. Wright *et al.* 2004; Han *et al.* 2005; Kerkhoff *et al.* 2006; Reich *et al.* 2010; Yan *et al.* 2016a). For example, Niklas and Cobb (2006) suggested that the scaling exponents of woody and herbaceous species are, on average 2/3 and 3/4, respectively. Based on an extensive worldwide collection of leaf N and P concentrations, Wright *et al.* (2004) claimed that the N vs. P scaling exponent was approximately 2/3. In contrast, using a larger leaf N and P data set consisting of 7,445 entries compiled by Reich and Oleksyn (2004), Niklas (2006) reports that the scaling exponent is 0.73, approaching 3/4 rather than 2/3. In addition, several other studies have indicated that the exponent was approximately 0.67 (Han *et al.* 2005), 0.72 (Kerkhoff *et al.* 2006), 0.78 (Zhao *et al*. 2016) or 1.0 (McGroddy *et al.* 2004). Based on what is to our knowledge the most comprehensive data to date, with 9,300 pairwise observations of leaf N and P concentrations, Reich *et al.* (2010) found similar 2/3 exponents across biomes, taxonomic divisions and angiosperm life forms, and therefore proposed the general 2/3-power law ($N \propto P^{2/3}$) across major plant groups and biomes. If true, a simple stoichiometric scaling relationship exists governing leaf stoichiometry and metabolism, despite differences among specific case studies.

However, similar to the inconstant scaling of leaf respiration with N and P (Rowland *et al.* 2017) and the biological quarter-power scaling (Savage *et al.* 2004), any N vs. P scaling relationship derived from a large global data set may hide important biological variations rooted in species-dependent, or region- or site-related differences. According to some stoichiometric scaling models, plant growth rates are purported to influence the N vs. P

scaling relationship (Sterner & Elser 2002; Niklas 2005; Ågren 2008). If true, plants from different functional groups or different geographical locations should have different growth rates due to specific evolutionary traits and environmental conditions, resulting in potential differences in their N vs. P scaling exponents. Additionally, according to some growth rate hypotheses (Elser *et al.* 2003; Güsewell 2004; Niklas 2006), growth rates are purported to be more closely correlated to P concentrations than N concentrations such that changes in P (and not N) demand or status are predicted to be a strong driver for variation in the numerical values of N vs. P scaling exponents.

To test the generality of the leaf N and P stoichiometry and the constancy of the leaf N vs. P scaling exponent, in this article we are firstly to explore the global leaf N and P stoichiometry that may be used as a base for the comparison of other individual studies. We then are to determine the N vs. P scaling exponent for different functional groups (i.e. woody species and herbs) and spatial scales (i.e. latitudinal zones, ecoregions/continents, and local sites) to evaluate whether the numerical value of the governing scaling exponent varies as a function of species composition, spatial distribution, or other variables of interest (e.g. climate conditions, and soil relative N and P availabilities) as sometimes reported by others (Vitousek & Howarth, 1991; Reich & Oleksyn, 2004; Han *et al.* 2011; Norby *et al.* 2016). Furthermore, we explore the patterns of scaling exponent numerical variation across different sites to test whether the "global" N vs. P scaling relationship obscures site-related significant differences. We hypothesize that the scaling exponent at each site should reflect site-specific N vs. P stoichiometric relationships, because plants growing at the same site represent the characteristics shaped by the combination of local climatic conditions, geological processes, soil nutrient availabilities, and other environment factors.

GLOBAL DATA SET AND STATISTICAL ANALYSE

In order to carry out the aforementioned studies, we compiled a large and geographically comprehensive global dataset of pairwise leaf N and P concentration distributions, including global, regional, and site-level records for as many of the variables of interest as possible. We adopted only those records reporting paired N and P concentrations of green leaves with detailed location information, and excluded all records without site information or with unpaired N-P records. Using a detailed review of the literature, our own field sampling, and the open TRY data set (Table S1; https://www.try-db.org; Kattge *et al.* 2011), a total of 12,055 records were acquired spanning 486 sites worldwide, in which 142 sites had more than 10 records for each site and 94 sites had more than 20 records for each site. Duplicated records were removed. The data set included 3,441 terrestrial plant species in 1,342 genera and 222 families. All of the plant samples in the data set were collected during the growing season. We used the Flora of China (http://frps.eflora.cn/), Useful Tropical Plants (http://tropical.theferns.info/), Australian Native Plants (https://www.anbg.gov.au/index.html), and Wikipedia (https://en.wikipedia.org/wiki) to identify plant functional groups and verify taxonomic classifications.

We conducted similar statistical analysis to Reich *et al*. (2010). To perform data analyses,

we $\log_{10}$-transformed the N and P concentration data for all plants in the dataset, and then used reduced major axis (RMA) regression to determine the N vs. P scaling relationship (Warton *et al.* 2006) at four levels (i.e. species functional groupings, latitudinal zones, ecoregions, and individual sites). Therefore, we first classified plants into herbaceous and woody species, and further divided woody plants into coniferous, deciduous broad-leaved and evergreen broad-leaved woody species. We then grouped the data from sites into tropical (0-25°), temperate (25-50°) and boreal (>50°) zones, to compare the N vs. P scaling exponents among these zones. We also analysed the latitudinal patterns of the scaling exponent for each of the species functional groups but excluding those of coniferous plants because most of the coniferous plants in our data set were distributed in the temperate zone. Our data analysis was then focused on patterns among ecoregions (continents), including North America (the United States of America, Canada and Mexico), Europe (Spain, Greece, France, Ukraine, Czech, Germany, Poland, Belgium, the Netherlands, United Kingdom, Norway and Sweden), Asia (China, Malaysia, India, Sri Lanka, Kazakhstan and Indonesia), Oceania (Australia and New Zealand), Africa (South Africa, Uganda and Cameroon), and South America (Brazil, Bolivia and Venezuela). Lastly, we analysed the N vs. P scaling relationships at each site (with $n \geqslant 10$ and $n \geqslant 20$ records) and quantified the numerical variation of the scaling exponent across different sites.

We used a likelihood-ratio test to evaluate the heterogeneity of RMA regression exponents within the aforementioned levels of analyses (Warton *et al.* 2006). Additionally, we performed general linear regressions to explore the changes in the scaling exponents with the geometric mean N and P concentrations and N:P ratios, using the statistical package R2.15.2 (R Development Core Team, 2015).

GLOBAL LEAF N and P STOICHIOMETRY ACROSS DIFFERENT SCALES

We used the above-described global dataset of 12,055 pairwise leaf N and P concentration records to characterize large-scale leaf N and P stoichiometry by functional group, latitudinal zone, eco-region, and site. The geometric mean values of leaf N and P concentrations and N:P mass ratios of the pooled data were 18.9 mg g^{-1} and 1.2 mg g^{-1}, and 15.8, respectively, but these numerical values differed significantly among the contrasting functional groups (Table 1). Compared to woody plants, herbaceous plants showed significantly higher N and P concentrations (21.72 mg N g^{-1} vs. 18.22 mg N g^{-1}; 1.64 mg P g^{-1} vs. 1.10 mg P g^{-1}), and lower N:P ratios (13.3 vs. 16.6). The mean leaf N (and P) concentrations of coniferous, deciduous broad-leaved, and evergreen broad-leaved woody species were 12.13 (and 0.98), 21.13 (and 1.37), and 15.45 (and 0.79) mg g^{-1}, respectively. The corresponding N:P ratios for the three woody species groups were 12.4, 15.4, and 19.5, respectively.

The leaf N and P stoichiometry also changed significantly with latitude. For the pooled data, the leaf N and P concentrations significantly increased from the tropical to boreal regions, but N:P ratios decreased (Table 2). Specifically, the geometric mean value of leaf N concentration was 17.41 mg g^{-1} in the tropical region, 19.24 mg g^{-1} in the temperate region, and 19.83 mg g^{-1} in the boreal region. The geometric mean value of leaf P concentration was

0.83 mg g^{-1} in the tropical region, 1.28 mg g^{-1} in the temperate region, and 1.49 mg g^{-1} in the boreal region. The geometric mean value of leaf N:P mass ratio was 21.0, 15.1, and 13.2 in the tropical, temperate and boreal regions, respectively. For each of the functional groups, the latitudinal patterns of N-P stoichiometry were generally consistent with the pooled data set, i.e. leaf N and P concentrations increased, but leaf N:P ratios decreased from tropical, to temperate, to boreal regions (Table 2).

Furthermore, there are remarkably differences in leaf N-P stoichiometry across different ecoregions (six continents) (Table 3). The geometric mean values of leaf N concentrations were 18.48 mg g^{-1}, 20.79 mg g^{-1}, 19.33 mg g^{-1}, 10.01 mg g^{-1}, 10.32 mg g^{-1}, and 18.51 mg g^{-1} for North America, Europe, Asia, Oceania, Africa, and South America, respectively. The respective geometric mean values of leaf P concentrations were 1.46 mg g^{-1}, 1.54 mg g^{-1}, 1.25 mg g^{-1}, 0.46 mg g^{-1}, 0.51 mg g^{-1}, and 0.69 mg g^{-1}, and the geometric mean values of leaf N:P mass ratio were 12.7, 13.5, 15.5 21.5, 20.4, and 26.7, respectively.

At different study sites, the leaf N-P stoichiometry also showed statistically significant differences. The site-level geometric mean values of leaf N and P concentrations and N:P mass ratios exhibited large variations among 142 sites with records of $n \geq 10$, ranging between 4.6 and 30.5 mg g^{-1} for N, 0.16 and 2.83 mg g^{-1} for P, and 6.3 and 35.4 for N:P, with respective geometric mean of 17.8 mg g^{-1}, 1.1 mg g^{-1}, and 15.8 (Fig. 1).

In short, in this section we documented the numerical values of the global leaf N and P stoichiometry by functional group, latitudinal zone, eco-region, and local site, which reveals a large variation in the leaf N and P concentrations and N:P ratios biologically and ecologically. Our results supported the general patterns of leaf N and P stoichiometry reported by Reich & Oleksyn (2004) and the numerical values could be used as a base for comparing other individual studies with the global averages documented here.

VARIATION IN THE LEAF N-P SCALING EXPONENT

Leaf N-P scaling exponents across different scales

In this section, we examine whether the leaf N-P scaling exponent varies among plant functional groups, latitudes, ecoregions, and local sites. As shown in Figure 2 and Table 1, the scaling exponent for the pooled data was 0.678 (95% CI = 0.669, 0.688), and thus statistically indistinguishable from 2/3. However, the numerical values of the scaling exponent differed significantly among the contrasting functional groups (Fig. 2). Compared to woody plants, herbaceous plants showed numerically lower N vs. P scaling exponents (0.659 vs. 0.705). The scaling exponents for coniferous, deciduous broad-leaved, and evergreen broad-leaved woody species were 0.610, 0.712, and 0.731, respectively (Fig. 2 and Table 1).

The leaf N-P scaling exponents also showed significant latitudinal differences. For the pooled data, the scaling exponents decreased from 0.747 in the tropical region, to 0.715 in the temperate region, and to 0.603 in the boreal region (Table 2 and Fig. S1a). For each of the functional groups, the latitudinal patterns of the scaling exponents were generally consistent with the pooled data set, i.e. the N vs. P scaling exponents decreased from tropical, to temperate, to boreal regions (Table 2 and Fig. S1b-d). For example, the exponent of evergreen

broad-leaved woody species group decreased from 0.783 in the tropical region, to 0.689 in the temperate region, to 0.643 in the boreal region. The numerical values of the deciduous broad-leaved woody species group in the tropical (0.704) and temperate (0.766) regions were much higher than those in the boreal region (0.424). Similarly, the scaling exponent of the herbaceous species group in the temperate region was statistically significantly higher than that in the boreal region (0.681 vs. 0.609).

Further investigation indicated a large difference in the leaf N-P scaling exponents across different ecoregions (six continents). The respective values of the scaling exponents in North America, Europe, Asia, Oceania, Africa and South America were 0.603, 0.672, 0.712, 0.786, 0.835, and 1.071 (Fig. 3 and Table 3).

The data of species growing in different sites manifested statistically significant differences in the numerical values of the leaf N-P scaling exponents. When the data from all 142 sites were pooled, the overall N vs. P scaling exponent was 0.664, or approximately 2/3 ($p > 0.05$). However, when scaling analyses were performed for each site, the numerical values of the 142 individual exponents showed a log-normal distribution with a mean value of 0.841 (a geometric mean of 0.804) and ranged from 0.366 to 1.928 (Fig. 4). Similarly, when only sites with larger sample sizes were considered (sites for which sampling records were $n \geq 20$, a total of 94 individual sites), statistically significant differences in the scaling exponents were detected, i.e., numerical values ranged between 0.441 and 1.492 with an average of 0.817 (Fig. S2b).

In summary, our data reveal large differences in the numerical values of leaf N vs. P scaling exponent that are dependent on species functional groups, ecoregions, and sample sites, although the numerical value when all records are pooled is close to 2/3.

Possible mechanisms of the different N-P scaling exponents

As shown in the previous section, an extensive analysis of a large worldwide data set consisting of 12,055 records shows that the numerical value of the exponent governing the leaf N vs. P scaling relationship is approximately 2/3 when all species are pooled. This is consistent with the finding of Reich *et al*. (2010). However, more detailed analyses of the same data set show that statistically significant differences exist in the exponents governing the leaf N vs. P scaling relationships depending on the functional group, latitudinal zone, ecoregion, or local site conditions being considered. These results show that the overall N vs. P scaling relationship derived from any "global data set" likely hides variation that is biologically (and thus ecologically) important, particularly with regard to modelling N and P dynamics on the whole ecosystem or site-specific levels.

The data presented here also shed some light as to why variations in N and P scaling relationships exist, although a detailed study of causalities is out of the scope of this paper. For example, the scaling exponents governing the N vs. P relationship are negatively correlated with leaf P concentration and positively correlated with N:P ratios but not significantly related to leaf N concentration (Fig. 5). We speculate that leaf P concentration play a pivotal role in "shaping" the numerical values of the N vs. P scaling exponent, i.e., metabolic requirements for P mainly account for scaling differences across different

functional groups, latitudinal zones, and the six continental ecosystems. This speculation resonates with previous studies reporting that changes in N:P ratios are mainly driven by variations in P concentration (Niinemets & Kull, 2003; Xie *et al*. 2003; Güsewell 2004).

In this regard, the influence of the requirement for P on growth rates might have the most influence on variations in the scaling exponents across functional groups. For example, compared to woody species, herbaceous species tend to be small-sized and have higher growth rates (Niklas, 1994; Güsewell & Koerselman 2002). According to the growth rate hypothesis of Sterner and Elser (2002), plants with higher growth rates are predicted to have higher P demands and lower N:P mass ratios (Delgado-Baquerizo *et al.* 2016). Our data reveal that herbaceous species have higher leaf P concentrations and lower N:P ratios (Table 1; see also see also Kerkhoff *et al.* 2006), which may account for N vs. P scaling exponents with lower numerical values (see Fig. 5). Similarly, compared to evergreen broad-leaved plants, deciduous broad-leaved plants tend to have low leaf longevity and rapid leaf growth rates (Chapin & Shaver 1989; van Ommen Kloeke *et al.* 2012; Díaz *et al.* 2016), resulting in high P demands and low N:P ratios. This difference may be responsible for the numerically smaller scaling exponents in deciduous relative to evergreen broad-leaved plants. In contrast, the numerically smaller N-P scaling exponents observed for coniferous species relative to broad-leaved woody species might reflect leaf morphological and anatomical characteristics in addition to P-related growth rate. The specific leaf area of conifers is generally smaller than that of broad-leaved species (Ackerly & Reich, 1999; Reich *et al.* 1999), which may result in relatively lower nutrient demands, especially for N (Table 1) (Ghimire *et al.* 2017). In addition, coniferous species are mostly distributed in cold habitats that may require the storage of lipid P in thick and narrow leaves for cold resistance (Chapin *et al.* 1986). Thus, compared to broad-leaved woody species, coniferous species tend to have low N:P ratios and thus numerically lower N vs. P scaling exponents (Table 1).

Species composition, P-related growth rates, and soil relative nutrient availabilities collectively appear to be the most important factors governing the numerical values of N vs. P scaling exponents across latitudinal zones. Plant functional group traits correlate significantly with the latitudinal pattern of leaf N and P concentrations and N:P ratios (Han *et al.* 2011) and thus likely control leaf N vs. P scaling relationships across latitudinal zones. In our global data set, evergreen broad-leaved trees dominate tropical regions, deciduous broad-leaved trees and herb plants co-dominate temperate regions, and conifer and herb species are more frequent than other plant species groups in boreal regions (Fig. 6a). In accordance with the aforementioned differences in the N-P scaling exponent across functional groups (Table 1), these distinct species groupings explain some but clearly not all of the latitudinal patterns of the N vs. P scaling exponent for each of the specific functional groups (i.e. evergreen broad-leaved woody species, and deciduous broad-leaved woody species and herbs). Other factors are likely involved. For example, the length of the growing season, and thus leaf longevity tend to decrease from the tropics to boreal regions, resulting in higher leaf growth rates and higher P-demands particularly in the growing season with increasing latitude (van Ommen Kloeke *et al.* 2012; Yan *et al.* 2016b). Furthermore, soil P availability relative to N availability tends to increase with increasing latitude or from the humid to arid regions, resulting in

decreasing leaf N:P ratios (Vitousek & Howarth 1991; Reich & Oleksyn 2004; Norby *et al.* 2016; Mariotte *et al*. 2017). These trends help to explain why the numerical values of the N vs. P scaling exponent decline from the tropics to higher latitudes for each of the major plant functional groups.

Species composition and soil relative nutrient availability are additional factors that are related with variation of the N vs. P scaling exponent across different ecoregions (continents) because they influence the N and P stoichiometry (Yang *et al*. 2015). For example, herbs and conifers are especially well represented in North America and Europe compared to the other four continents, whereas broad-leaved deciduous species dominate the species composition in Asia and evergreen broad-leaved species dominate Oceania, Africa, and South America (Fig. 6b). Considering that N vs. P scaling exponents differ as a function of functional groupings, we suggest that the biases in the species composition observed for the different continents are an important contributor to the differences in the numerical values of N vs. P scaling exponents. Furthermore, previous studies have shown that soil relative nutrient availability differs among the six continents. According to the world map of nutrient limitations (Wang *et al.* 2010; Norby *et al.* 2016) and soil P distribution (Yang *et al.* 2014), European and North American sample sites are mainly N-limited, the Asian sample sites are located in both N-limited and P-limited regions, whereas sample sites in South America, Africa, and Oceania are mostly located in P-limited regions. Moreover, P limitation tends to increase with elevated N:P ratios, whereas N limitation increases with declining N:P ratios (Xie *et al*. 2003; Güsewell 2004). This feature, even in isolation, could explain the lower N vs. P scaling exponents observed for sample sites in North America and Europe compared to those in Africa, Oceania and South America.

Based on the Global Gridded Soil Phosphorus Distribution Maps (Yang *et al.* 2014), we extracted the total P density in the top 50 cm soil and analysed the relationships between the leaf N vs. P scaling exponent and soil total P density at the different scales of globe, latitude range, and continent. We found that the scaling exponent tended to decrease with increasing soil P density (Fig. S3, r^2=0.28, p=0.024). This result further demonstrates the crucial role of soil P in influencing the leaf N vs. P scaling exponent (Zhou *et al*. 2015). In addition, plants tend to uptake excess N (i.e. luxury consumption of N) when soil P availability is deficient (Garten, 1976; Ågren, 2004 & 2008) and *vice versa* (Chapin, 1980; Sistla *et al*. 2015). Excess uptake of elements could mask the stoichiometric requirements to varying degrees and dramatically modify the N-P scaling relation. Generally, excess uptake of N for P-limited plants causes a higher scaling exponent of leaf N vs. P, whereas excess uptake of P for N-limited plants results in a lower scaling exponent (Ågren, 2008). Moreover, leaf N concentration could occasionally be negatively correlated with leaf P concentration in the case of 'luxury' N uptake (Güsewell, 2004). However, given the pervasiveness of N and P limitation in terrestrial ecosystems (Elser *et al.* 2007; Sullivan *et al.* 2014) and the difficulty in detecting the magnitude of excess nutrient uptake, the exact extent of N vs. P scaling flexibility resulted from the excess nutrient uptake in various nutrient limited sites may hardly be evaluated. Finally, as most of the sample sites in Europe and North America are located at high latitudes and regarded as N-limited, whereas the South American sample sites are mainly

located at low latitudes generally limited by P, the variations in the scaling exponent across these continents are coincident with the aforementioned latitudinal patterns.

Our results have revealed large variations of the leaf N and P stoichiometry and the N vs. P scaling exponent, although the fundamental mechanisms underpinning these patterns remain not well interpreted. Initially, the 3/4 or 2/3 "power law" empirically proposed by studies with limited data or pooled data combining all the functional groups which primarily ignored the phylogeny of plants, were in lack of convincing theoretical foundation (Wright *et al.* 2005; Niklas *et al.* 2005; Niklas & Cobb, 2006; Reich *et al.* 2010). Actually, 13 years ago Savage *et al.* (2004) recognized the similar variability in the allometric scaling exponent in biology by synthesizing studies of basal metabolic rates. Due to the lack of supporting data of soil nutrient availability for each record in our dataset, we failed to build strong correlations between leaf N vs. P scaling exponents and soil parameters at site levels. Hence, extensive data of paired N-P concentration of leaves and soils with supporting biogeographic and physiological information are in great need to provide more evidence for the explanation of the variation in the scaling exponent.

CONCLUSIONS

Our results documented detailed information on leaf N and P concentrations and N:P ratios of different functional groups, latitudinal zones and ecoregions. Leaf N and P concentrations of herbaceous plants were significantly higher than for woody plants, which showed decreasing trends from boreal to tropical regions. Among six continents, Europe had the highest N and P concentrations and Oceania showed the smallest values. Especially, our data indicated large differences in the numerical values of leaf N vs. P scaling exponents dependent on species functional groups, ecoregions, and sample sites, although the numerical value for the exponent when all records were pooled was close to 2/3. Compared to woody species, herbaceous species have a lower N vs. P scaling exponents (0.659 vs. 0.705). Among woody species, conifers have the lowest scaling exponent (0.610), whereas deciduous and evergreen broad-leaved woody species have the highest values (0.712 and 0.731, respectively). The numerical values of exponents manifest a significant latitudinal pattern with decreasing values from tropical to temperate to boreal regions. Notable differences in the scaling exponent also occur across North America, Europe, Asia, Oceania, Africa, and South America (i.e., α = 0.603, 0.672, 0.712, 0.786, 0.835 and 1.071, respectively). In addition, the numerical values of the exponent differed as a function of sample site, with a geometric mean value of 0.804, ranging from 0.366 to 1.928. These results showed that there is no canonical numerical value for the N vs. P scaling exponent and that the analysis of pooled data for this scaling relationship may hide biologically and ecologically significant variation. Our findings have important implications for predicting plant growth rate and ultimately vegetation productivity, for helping parameterize vegetation-climate models (Wright *et al*. 2005; Niklas, 2006; Tang *et al.* 2017), and for increasing our understanding of plant adaptation and evolution (Kerkhoff *et al*. 2006). Our results also suggest that we need to incorporate specific exponents into scaling leaf N to P in plant growth and ecosystem functioning models according to functional groups,

biogeographic regions, and ecosystem nutrient availabilities.

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FUNDING

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565 **Table 1.** Summary of reduced major axis (RMA) regression results between leaf N and leaf P
566 concentrations, e.g., $\log_{10}$ leaf N = α $\log_{10}$ leaf P + $\log_{10}\beta$, the statistics of leaf N and P
567 concentrations, and the N:P ratios in terrestrial plants for different functional groups. Note:
568 woody plants were divided into three groups: coniferous gymnosperms, and two angiosperms
569 groups, deciduous broad-leaved and evergreen broad-leaved woody. Mean indicates the
570 geometric mean, and *n* is the number of observations. Each regression relationships were
571 statistically significant with $p<0.05$. Different letters denote significant difference ($p<0.05$)
572 among latitude zones based on a likelihood-ratio test.

Functional group	*n*	α_{RMA} (95% CI)	r^2	N mean (mg g^{-1})	P mean (mg g^{-1})	N:P mean
All	12, 055	0.678b (0.669, 0.688)	0.33	18.93	1.20	15.8
Functional group						
Herb	2, 776	0.659bc (0.637, 0.681)	0.20	21.72	1.64	13.3
Woody	8, 888	0.705a (0.693, 0.717)	0.34	18.22	1.10	16.6
Conifer woody	526	0.610c (0.574, 0.648)	0.50	12.13	0.98	12.4
Deciduous broadleaf	5, 035	0.712a (0.695, 0.730)	0.22	21.13	1.37	15.4
Evergreen broadleaf	3, 267	0.731a (0.710, 0.753)	0.29	15.45	0.79	19.5

573

574

575 **Table 2.** Summary of reduced major axis (RMA) regression results between leaf N and leaf P
576 concentrations (e.g. $\log_{10}$ leaf N = α $\log_{10}$ leaf P + $\log_{10}\beta$), the statistics of leaf N and P
577 concentrations, and the N:P mass ratio in terrestrial plants along the latitudinal zones. The
578 exponent of herbs in the tropical zone was excluded in the comparison due to the paucity of
579 samples in our data set. We also did not consider the latitudinal pattern of conifers because
580 most of the coniferous samples in our data set were distributed in the temperate zone. All the
581 plants including conifers and tropical herbs were pooled together during the evaluating of the
582 latitudinal pattern for all plants. Mean indicates geometric mean, and *n* is the number of
583 observations. Each regression relationships were statistically significant with $p < 0.05$.
584 Different letters denote significant difference ($p < 0.05$) among latitude zones based on a
585 likelihood ratio test.

Latitudinal zone	*n*	α_{RMA} (95% CI)	r^2	Nmean (mg g^{-1})	Pmean (mg g^{-1})	N:Pmean
Latitude zone for all plants						
0-25° (tropical)	2, 278	0.747a (0.721, 0.775)	0.22	17.41	0.83	21.0
25-50° (temperate)	8, 225	0.715b (0.703, 0.728)	0.38	19.24	1.28	15.1
>50° (boreal)	1, 470	0.603c (0.576, 0.631)	0.21	19.83	1.49	13.2
Latitude zone for evergreen broad-leaved plants						
0-25° (tropical)	1, 679	0.783a (0.750, 0.818)	0.17	17.01	0.78	21.9
25-50° (temperate)	1, 350	0.689b (0.663, 0.716)	0.48	13.78	0.76	18.2
>50° (boreal)	219	0.643b (0.584, 0.707)	0.49	15.23	1.27	12.0
Latitude zone for deciduous broad-leaved plants						
0-25° (tropical)	313	0.704a (0.642, 0.772)	0.32	19.77	1.10	18.0
25-50° (temperate)	4, 218	0.766a (0.746, 0.787)	0.23	21.06	1.35	15.6
>50° (boreal)	469	0.424b (0.388, 0.464)	0.03	22.89	1.81	12.6
Latitude zone for herbaceous plants						
25-50° (temperate)	2, 039	0.681a (0.655, 0.708)	0.19	22.38	1.74	12.9
>50° (boreal)	673	0.609b (0.570, 0.651)	0.21	20.08	1.39	14.3

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588 **Table 3.** Summary of reduced major axis (RMA) regression results between leaf N and leaf
589 P concentrations, e.g., $\log_{10}$ leaf N = α $\log_{10}$ leaf P + $\log_{10}\beta$, the statistics of leaf N and P
590 concentrations, and the N:P ratios in terrestrial plants across different continents. Note: each
591 continent only contained those countries that had sampling sites in our data set (for details,
592 see text). Mean indicates geometric mean, and *n* is the number of observations. Each
593 regression relationships were statistically significant with $p<0.05$. Different letters denote
594 significant difference ($p<0.05$) among latitude zones based on a likelihood ratio- test.

Region	*n*	α_{RMA} (95% CI)	r^2	N.mean (mg g^{-1})	P.mean (mg g^{-1})	N:P.mean
Global	12055	0.678d (0.669, 0.688)	0.33	18.94	1.20	15.8
North America	706	0.603e (0.563, 0.646)	0.13	18.48	1.46	12.7
Europe	1852	0.672d (0.646, 0.699)	0.26	20.79	1.54	13.5
Asia	7951	0.712c (0.699, 0.726)	0.30	19.33	1.25	15.5
Oceania	380	0.786b (0.741, 0.834)	0.66	10.01	0.46	21.5
Africa	100	0.835b (0.750, 0.930)	0.71	10.32	0.51	20.4
South America	942	1.071a (1.011, 1.134)	0.19	18.51	0.69	26.7

595 The countries located in the six continents were as follows: North America: the United States
596 of America, Canada, Mexico; Europe: Spain, Greece, France, Ukraine, Czech, Germany,
597 Poland, Belgium, the Netherlands, United Kingdom, Norway, Sweden; Asia: China,
598 Malaysia, India, Sri Lanka, Kazakhstan, Indonesia; Oceania: Australia, New Zealand;
599 Africa: South Africa, Uganda, Cameroon; South America: Brazil, Bolivia, Venezuela.

FIGURE LEGENDS

Figure 1. Frequency distribution of leaf N and P contents and N:P ratio of samples from the 142 sites with > 10 records. (a) leaf N content; (b) leaf P content; and (c) leaf N:P ratio.

Figure 2. Relationships between leaf N and leaf P concentrations in terrestrial plants among functional groups. (a) all species pooled together, (b) herbaceous plants, (c) woody plants pooled together, and (d) woody plants classified by lifeforms (EB, evergreen broad-leaved; DB, deciduous broad-leaved; and C, conifers). Scaling exponents (α) were calculated from the RMA regression between leaf N and leaf P concentrations, e.g. $\log_{10}$ leaf N = α $\log_{10}$ leaf P + $\log_{10}\beta$. N, P and N:P indicate the geometric mean values of leaf N concentrations, P concentrations and N:P ratio, respectively. Numbers in square brackets denote the lower and upper 95% confidence limits of the scaling exponents.

Figure 3. Relationship between leaf N and leaf P concentrations in terrestrial plants among six ecoregions (continents). Scaling exponents (α) were calculated from the RMA regression between leaf N and leaf P concentrations, e.g., $\log_{10}$ leaf N = α $\log_{10}$ leaf P + $\log_{10}\beta$. N, P and N:P indicate the geometric mean values of leaf N concentration, P concentration and the N:P ratio, respectively. Note: each continent only contains those countries with sampling sites that were documented in our data set. The countries located on the six continents were as follows: (a) North America: the USA, Canada, and Mexico; (b) Europe: Spain, Greece, France, Ukraine, Czech, Germany, Poland, Belgium, the Netherlands, England, Norway, and Sweden; (c) Asia: China, Malaysia, India, Sri Lanka, Kazakhstan, and Indonesia; (d) Oceania: Australia and New Zealand; (e) Africa: South Africa, Uganda, and Cameroon; and (f) South America: Brazil, Bolivia, and Venezuela. Numbers in square brackets indicate the lower and upper 95% confidence limits of the scaling exponents.

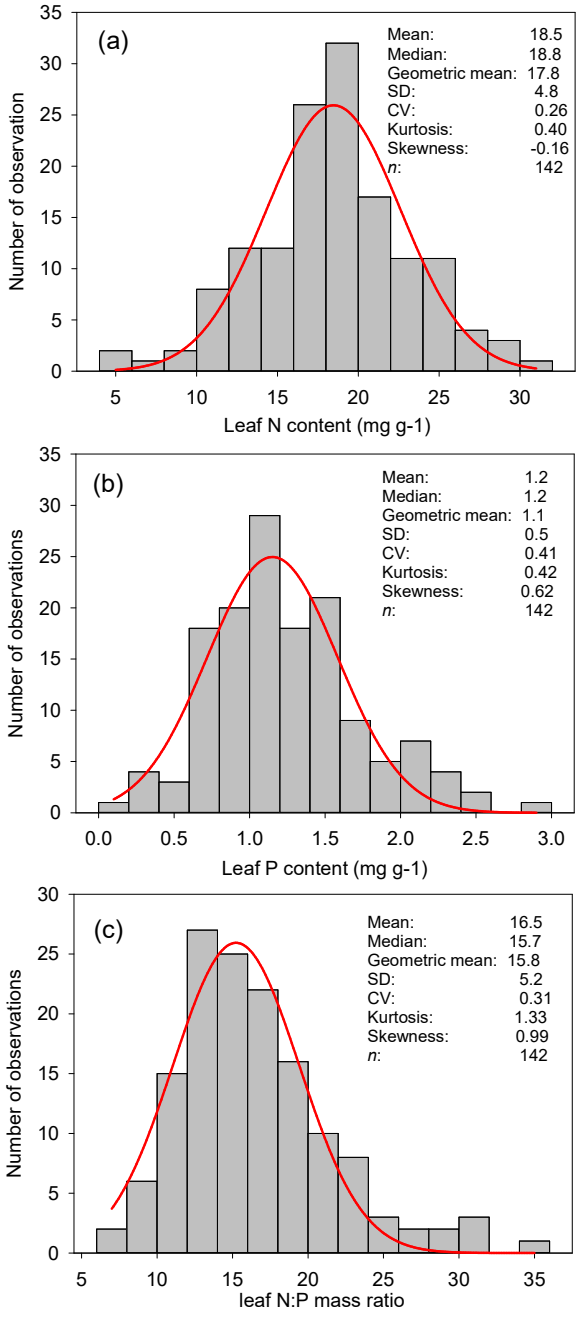
Figure 4. The leaf N to P scaling at 142 sites with more than ten records. **(a)** Relationships between leaf N and P concentrations with overall RMA-regression line (red) and separate RMA-regression lines for sites (black); **(b)** Frequency distribution of the scaling exponents from the 142 sites (slopes of the black lines in a). All regression slopes were significantly larger than zero (p<0.05).

Figure 5. Relationships between the N to P scaling exponents and leaf N, P and N:P mass ratios at different scales. (a) Relationships between the N to P scaling exponents and leaf N content; (b) relationships between the N to P scaling exponents and leaf P content; and (c) relationships between the N to P scaling exponents and N:P mass ratio. The error bars indicate the 95% confidence interval (CI) of the scaling exponents. Leaf N and P content and N:P ratios were derived from the geometric

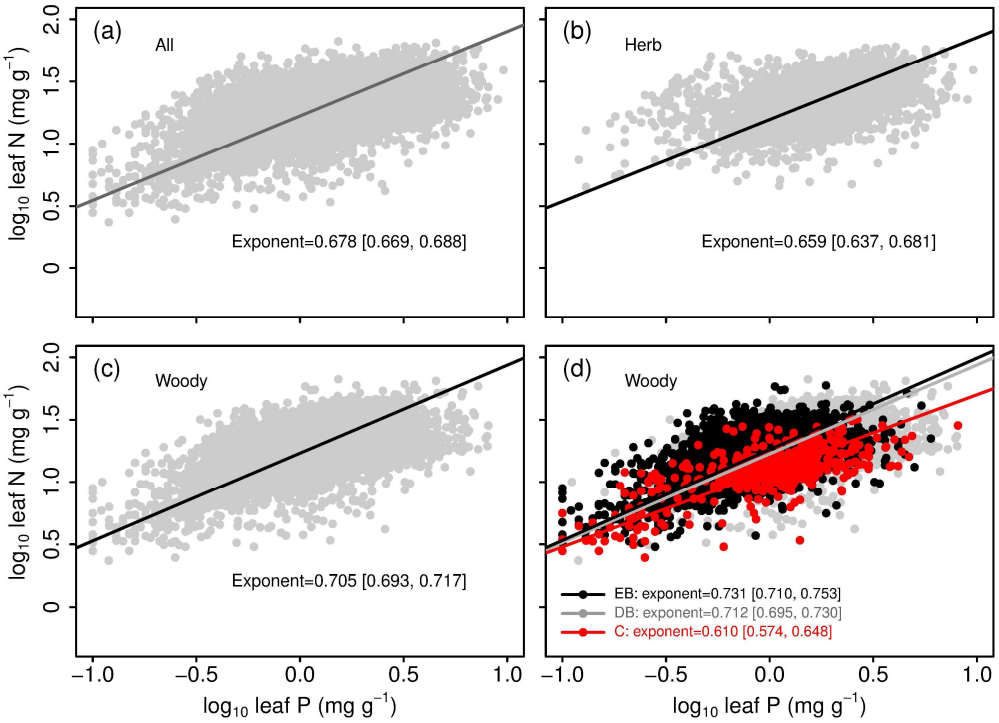
means of the analysed samples during each scaling relationship analysis. Scaling exponents (α) were calculated from the RMA regression between leaf N and leaf P concentrations, e.g., $\log_{10}$ leaf N = α $\log_{10}$ leaf P + $\log_{10}\beta$. The black, red, blue and green dots in the legend respectively represent mean values from five functional group level (cf. Table 1), six continents, eleven latitudinal zones (cf. Table 2) and one global level.

Figure 6. Changes in species composition along (a) the latitudinal zones and (b) across six continents. The four functional groups (herb, evergreen broad-leaved woody species, deciduous broad-leaved woody species and conifers) occupied most of the sample cases, whereas some species (e.g., fern) or unknown plants were not included in the analysis.

Figure 1

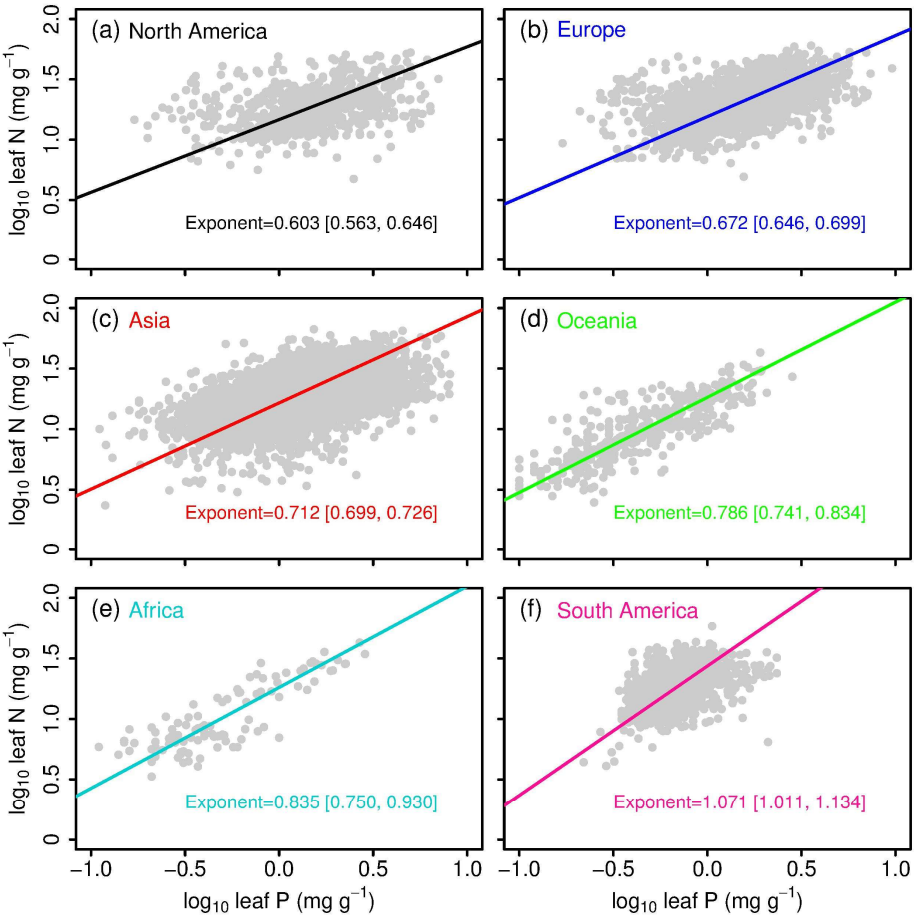

(a)
Mean: 18.5
Median: 18.8
Geometric mean: 17.8
SD: 4.8
CV: 0.26
Kurtosis: 0.40
Skewness: -0.16
n: 142
Number of observation
Leaf N content (mg g-1)
(b)
Mean: 1.2
Median: 1.2
Geometric mean: 1.1
SD: 0.5
CV: 0.41
Kurtosis: 0.42
Skewness: 0.62
n: 142
Number of observations
Leaf P content (mg g-1)
(c)
Mean: 16.5
Median: 15.7
Geometric mean: 15.8
SD: 5.2
CV: 0.31
Kurtosis: 1.33
Skewness: 0.99
n: 142
Number of observations
leaf N:P mass ratio

658 **Figure 2**



659

660 **Figure 3**



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663 **Figure 4**

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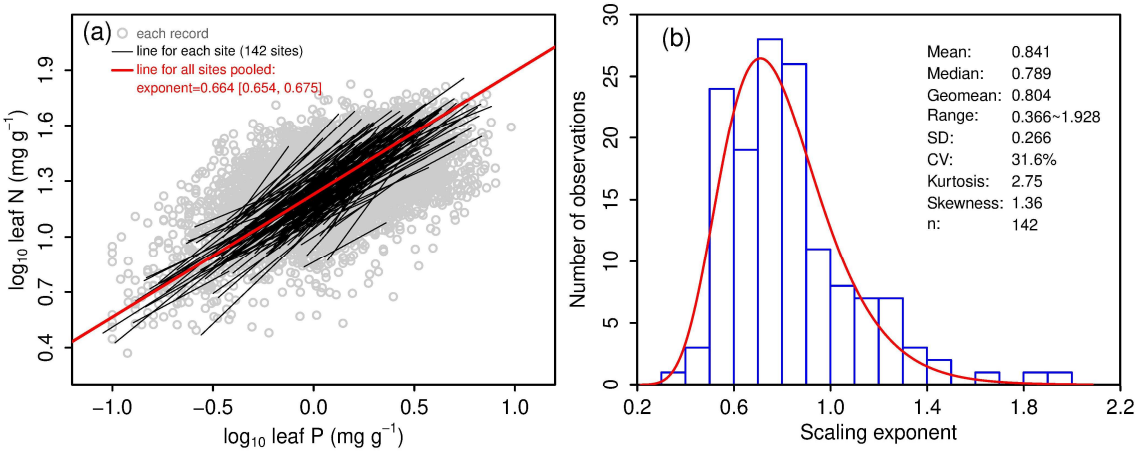
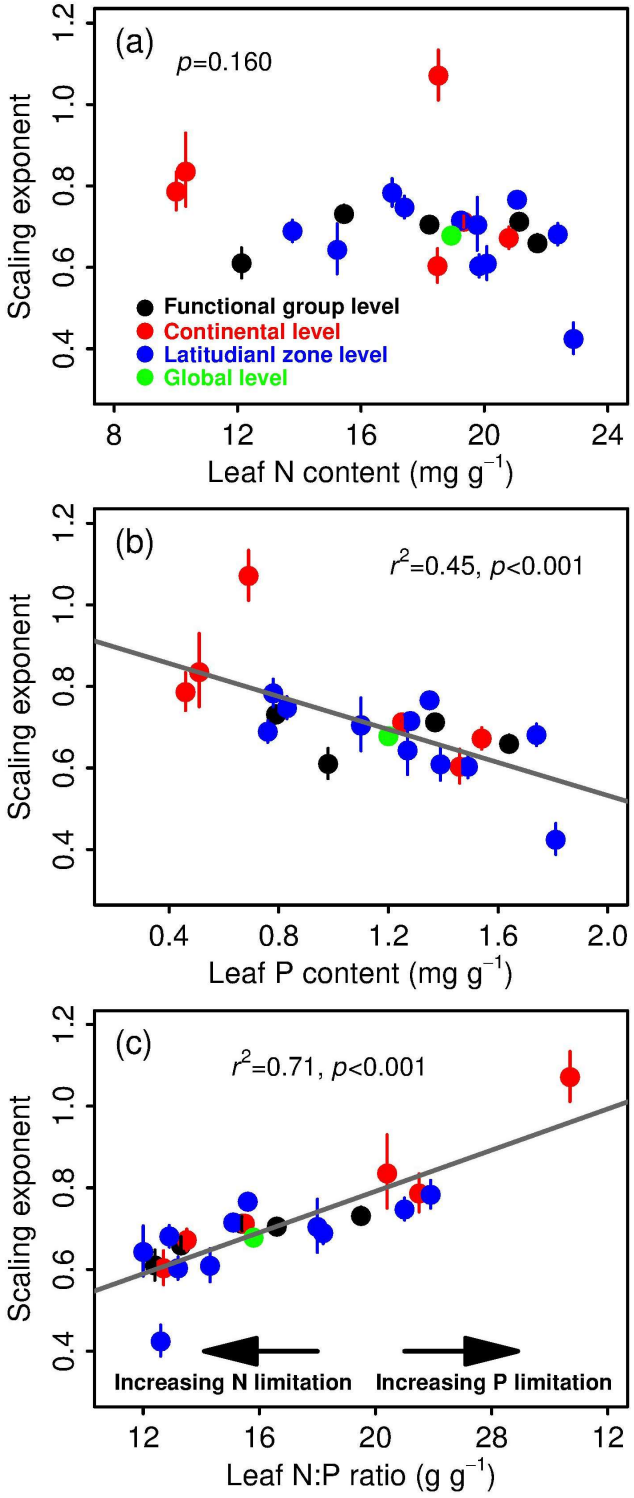


665 **Figure 5**



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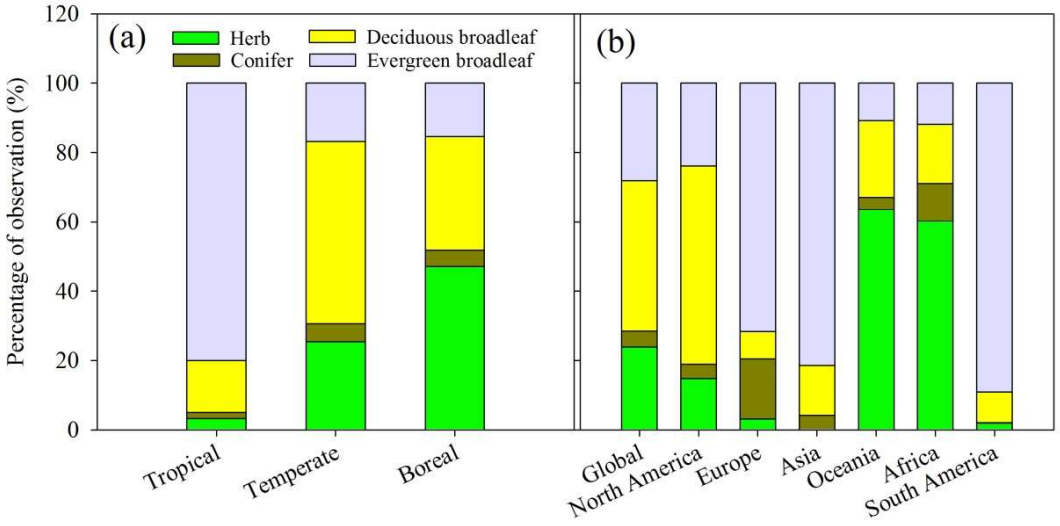
667

668 **Figure 6**



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SUPPORTING INFORMATION

Additional Supporting Information is available in the online version of the paper.

Tables S1. Data sets in TRY that contributed to our global leaf N and P data set

Figures S1. Relationships between leaf N and leaf P concentrations in terrestrial plants along the latitudinal zones classified by functional groups: (a) all the species pooled together, (b) evergreen broad-leaved woody species; (c) deciduous broad-leaved woody species; (d) herbaceous species. Relationships for coniferous woody plants along the latitudinal zones and herbaceous species in tropical zone were excluded due to the paucity of data.

Figures S2. The leaf N and leaf P scaling at 94 sites with sampling size of >20 records. **(a)** Relationships between leaf N and leaf P concentrations for 94 sites; and **(b)** frequency distribution of the scaling exponents from 94 sites.

Figures S3. Relationship between the leaf N and P scaling exponents and the total P density in the top 50cm soil at different scales of globe, latitude range, and continent.

Supplementary References

694 **SUPPORTING INFORMATION**

695

696 # Global leaf nitrogen and phosphorus stoichiometry and the scaling
697 # exponents

698

699 Di Tian[1], Zhengbing Yan[1], Karl J. Niklas[2], Wenxuan Han[3], Jens Kattge[4], Peter B.
700 Reich[5,6], Yongkai Luo[7], Yahan Chen[7], Zhiyao Tang[1], Huifeng Hu[7], Ian J. Wright[8],
701 Bernhard Schmid[9], Jingyun Fang[1*]

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724 **This file includes:**
725 **Tables S1**
726 **Figures S1 to S3**
727 **Supplementary References**

728 **Table S1.** Data sets in TRY that contributed to our global leaf N and P data set. *n*
729 indicates the number of samples imported to our dataset. References cited in this table
730 are attached below.

Dataset ID in TRY	*n*	Contributor	Reference	Dataset Name
1	100	Johannes Cornelissen	S1	Abisko & Sheffield Database
20	699	Ian Wright	S2	GLOPNET-Global Plant Trait Network Database
34	332	Jon Lloyd	S3	The RAINFOR Plant Trait Database
37	181	Johannes Cornelissen	S4	Sheffield Database
45	643	Eric Garnier	S5	The VISTA Plant Trait Database
50	11	Shipley Bill	S6	Leaf and Whole Plant Traits Database
51	35	Emily Swaine	S7	Tropical Plant Traits From Borneo Database
56	153	Peter van Bodegom	S8	Wetland Dunes Database
87	122	Ülo Niinemets	S9	Global Leaf Robustness and Physiology Database
88	281	Jenny Ordonez	S10	The Netherlands Plant Traits Database
90	115	Peter van Bodegom	Unpublished	Ukraine Wetlands Plant Traits Database
94	102	Peter Reich	S11	Global A, N, P, SLA Database
105	40	Gregoire Freschet	Unpublished	Traits from Subarctic Plant Species Database
130	934	Joseph Craine	S12	Global 15N Database
152	31	Peter Adler	S13	Functional Traits of Graminoids in Semi-Arid Steppes Database
166	3	Andreas Demey	S14	Traits of Hemiparastic Plants
193	520	Daniel Laughlin	S15	Plant Traits for Pinus and Juniperus Forests in Arizona

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Figure S1. Relationships between leaf N and leaf P concentrations in terrestrial plants along the latitudinal zones classified by functional groups: (a) all the species pooled together, (b) evergreen broad-leaved woody species; (c) deciduous broad-leaved woody species; (d) herbaceous species. Relationships for coniferous woody plants along the latitudinal zones and herbaceous species in tropical zone were excluded due to the paucity of data. Scaling exponents (α) were calculated from the RMA regression between leaf N and leaf P concentrations, e.g., $\log_{10}$ leaf N = α $\log_{10}$ leaf P + $\log_{10}\beta$. Numbers in square brackets denote the lower and upper 95% confident intervals of the scaling exponents.

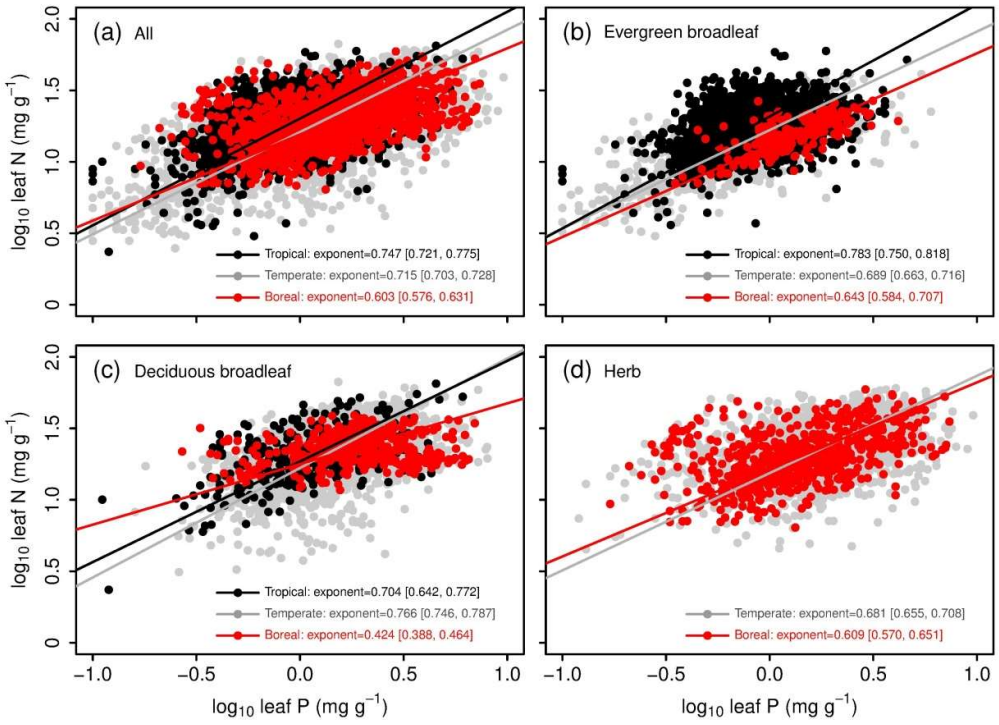


Figure S2. The leaf N and leaf P scaling at 94 sites with sampling size of >20 records. **(a)** Relationships between leaf N and leaf P concentrations for 94 sites; and **(b)** frequency distribution of the scaling exponents from 94 sites. Each black line in **(a)** indicates the scaling relationship at each site. Scaling exponents (α) were calculated from the RMA regression between leaf N and leaf P concentration, e.g., $\log_{10}$ leaf N = α $\log_{10}$ leaf P + $\log_{10}\beta$. Each regression relationships were statistically significant with p<0.05.

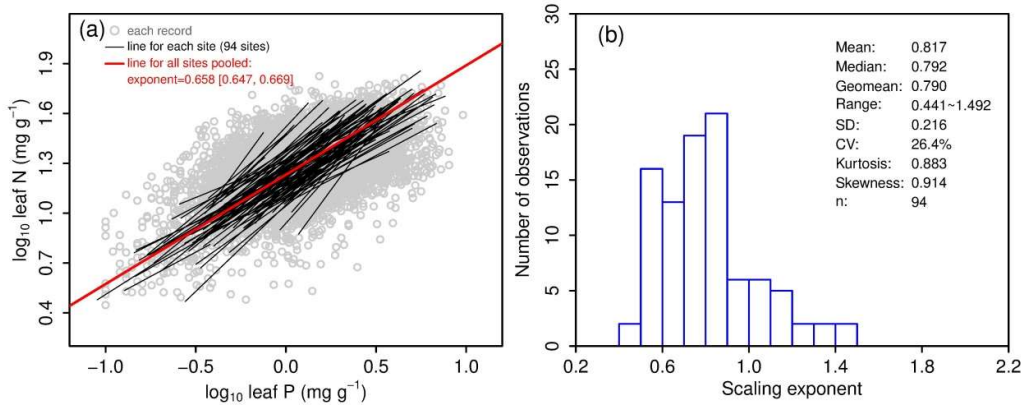
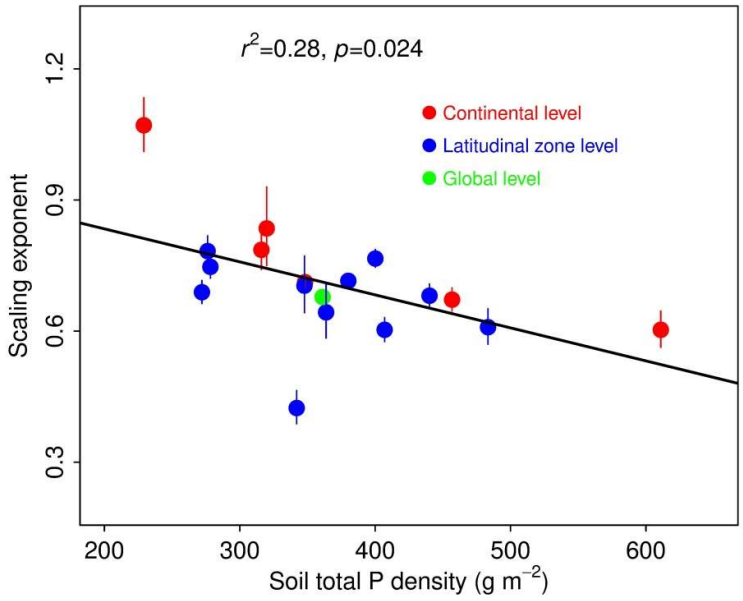


Figure S3. Relationship between the leaf N and P scaling exponents and the total P density in the top 50cm soil at different scales of globe, latitude range, and continent. Estimates of soil total P density were extracted from the Global Gridded Soil Phosphorus Distribution Maps at 0.5-degree Resolution at http://daac.ornl.gov. The error bars indicate the 95% confidence interval (CI) of the scaling exponents. The soil TP density was derived from the geometric mean of the analysed samples during each scaling relationship analysis. Scaling exponents (α) were calculated from the RMA regression between leaf N and leaf P concentrations, e.g., $\log_{10}$ leaf N = α $\log_{10}$ leaf P + $\log_{10}\beta$. The red, blue and green dots in the legend respectively represent mean values from six continents, eleven latitudinal zones (cf. Table 2) and one global level.



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